

Human Genes and Biocultural History in Southeast Asia



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SOUTHEAST ASIA is rich in human diversity. For example, this region (taken as comprising Burma, Laos, Thailand, Viet Nam, Kampuchea, Malaysia, the Philippines, and Indonesia, excluding Irian Jaya) contains over 800 languages (Grimes 1984). Southeast Asian ecological adaptations, cultures, and genetic patterns are also diverse. Much of this biocultural richness can be attributed to past cultural isolation related to varied topography and hence to the variety of ecological niches available. Part can be related to movements by more northerly peoples in recent millennia (Wurm and Hattori 1983). As I will argue, significant traces of unity within this Southeast Asian diversity may be related to human events that go back over 40,000 years ago.

In this essay I review aspects of the prehistoric roots of Southeast Asian biocultural unity, using genetic and other information. As we enter an era of increased interest in the components of human biological evolution (Baer 1993), critical genetic tests of their temporal and spatial causes will become more widespread (Peterson et al. 1993).

In the first section of this report, I examine language affiliations and describe how Mainland and Island Southeast Asia appear to be separate on linguistic grounds. Later I describe biocultural factors that appear to link, or unite, the mainland with the islands: genetic traits, cultural traits, geological history, and biogeography.

Among the questions underlying my approach are the following: Are today's Southeast Asians largely the product of the gradual increase and differentiation of small groups native to the region over the past 40,000 to 50,000 years? Or is their gene pool largely derived from the movement of outside groups at the expense of natives, either during the past 2000 years of proto-history and history or starting 6000 years ago with the postulated movement of Austronesian-speaking colonists from Taiwan (Bellwood 1985; but see Solheim 1984–1985)? While it seems unlikely that Southeast Asia was ever a "sealed box," we should keep in mind that some of its areas were more isolated than others and that the box's outlets and inlets were not random.

If, as I postulate, the major pattern of ancient Southeast Asian settlement was in

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situ expansion, then two possible concomitants deserve attention. One is the existence of a diverse language group with a homeland in Southeast Asia. The other is the persistence of close genetic relatedness among many Southeast Asians. I take up the question of language first.

LANGUAGE

The main language categories found in Southeast Asia today are Sino-Tibetan, Tai-Kadai, Austronesian, and Austroasiatic. On historical and linguistic grounds, the first three are thought to have originated outside of Southeast Asia (but see Terrell 1986 and Meacham 1991 on in situ development of Austronesian). The most likely homeland of Austroasiatic, however, is Mainland Southeast Asia (Diffloth 1974; Wurm and Hattori 1983, back of map 36).

Austroasiatic contains about 150 languages in Mainland Southeast Asia, classified into three main subgroups: Mon-Khmer, Viet-Muong, and Aslian (Matisoff 1983; but see Ruhlen 1991). A fourth subgroup is an outlier in northern India, and a fifth is found in the Nicobar Islands near the northwest tip of Sumatra.

Most of the Austroasiatic languages in Southeast Asia have relict distributions, resulting in large part from population movements or from domination by northerners during recent millennia. Yet Island Southeast Asia, the area between the Malay Peninsula and New Guinea and between Australia and Taiwan, contains no Austroasiatic languages today. While Benjamin (1987) has suggested that northern Sumatrans and some groups in the Mergui Archipelago once were Austroasiatic speakers, little evidence exists for Austroasiatic languages ever having been spoken in the rest of Indonesia, the Philippines, or North Borneo. Most of these latter areas today contain Western Malayo-Polynesian languages, a subgroup of Austronesian. Some areas of eastern Indonesia, however, contain Papuan languages.

All this may seem to suggest that Mainland and Island Southeast Asia never had a commonality of language. However, any existing commonality may have been overlaid by the advance of Malayo-Polynesian through the insular area. It is noteworthy that several words in nonagricultural Southeast Asian groups are distributed widely. "Batek" or "Batak" is a self-name for one group of the Semang hunter-gatherers in West Malaysia, for a highland swidden group in Sumatra, and for a hunter-gatherer group on Palawan Island. Also, "Karei" or "Kayai" is the name for the Semang thunder spirit and for a similar spirit among other hunter-gatherers or among agriculturalists in Malaya, Borneo, and the Philippines (Blust 1981). *Karei* may be a pre-Austroasiatic word. At any rate, both *Karei* and *Batak* are unlikely to be Western Malayo-Polynesian words because this language group is thought to have reached Malaya only some 2000 years ago (Bellwood 1985; Blust 1984–1985), long after Austroasiatic was established there.

Linguists have not hazarded estimates of the age of the Austroasiatic group as a whole (Diffloth 1974), although Benjamin's calculations (1989) suggest that the Aslian subgroup, spoken on the Malay Peninsula by hunter-gatherers and swidden cultivators, is over 4000 years old. If Austroasiatic as a whole is only some few millennia older, linguistic analysis of Austroasiatic is unlikely to provide clues about life in Southeast Asia during the formative period going back over 40,000 years ago. We might look, then, for a language group that is older than Austro-

asiatic on the mainland; but no obvious candidate seems to exist. A supertaxon of Southeast Asian language groups has been proposed, and may have explanatory power, but the issue has not been resolved (Reid 1984–1985; Ruhlen 1991 : 154; Solnit 1992).

In sum, language does not provide a strong link between Mainland and Island Southeast Asia today. Whether it did in the distant past is unknown and perhaps unknowable. This language disjunction between mainland and islands, however, may help to explain why prehistorians often consider the two parts of Southeast Asia separately (Bellwood 1985; Higham 1989).

GENETIC AND EPIGENETIC DATA SETS

In the long run, a combination of all relevant data is needed to arrive at an overview of Southeast Asian human evolution: data on morphology, genes, ecology, culture, disease patterns, and so on (for a discussion of this view, see, e.g., Yoder 1994 : 35–37).

At present, we must make do with less than this ideal approach. To take one example, both bones and genes are part of the human biological picture for Southeast Asia. Although osteological and dental data have generated interesting theories on Southeast Asian prehistory, they are independent of a gene-molecule approach. First, the genetic basis of skeletal traits is unknown, and thus the evolutionary forces acting on them are unknown. In other words, genes are descended from genes, but bones are not descended from bones. Second, typological models of morphology make a poor fit with the variability approaches of genetics. For the focus of this paper, a further problem arises in considering morphological alongside genetic data. While multi-trait human osteological studies often compare New Guinea, Australia, Japan, and China with Southeast Asia, they have been known to cover the mainland or island area haphazardly, to lump together people of different language families, or to ignore aboriginal Taiwanese (a test group for Austronesian cultural origins). Also, unusual connections have been reported, such as the people of Laos being closer to those of Java and Sulawesi than to those of Burma or China (Hanihara 1993 : 41–42). For these and other reasons, morphological data sets have not provided a comprehensive picture of Southeast Asian biological history, especially for early periods, for which fossil remains are scarce (see, e.g., Bräuer 1992 : 409).

Genetic data sets also have their limitations. For example, though genes fuel the mechanisms of evolution, data on genetic variation and change cannot easily be converted into data on archaeological variation and history (Marks 1994). No amount of genetic information, of the kinds now available, will tell us what the people of 40,000 years ago looked like or how they lived. Genetics provides no resolution to the question of the first appearance of modern *Homo sapiens* in Southeast Asia, which continues to be problematic (Brown 1992).

HUMAN GENES IN SOUTHEAST ASIA

The traditional genetic method of analyzing regional relationships depends on knowing the frequencies of gene variants (alleles) in populations. Several prob-

lems with this methodology are relevant to Southeast Asia. First, the frequencies of alleles are known for only a few Southeast Asian populations. They provide scant data to assess genetic relationships within the region by the method of genetic distance analysis and to present the results in the form of trees, or dendrograms. Cavalli-Sforza and his colleagues (1992:616) provide a hallmark of this approach. However, methods of "tree" analysis are known to vary in their outcomes, for example, placing native Australians close to Indonesians by one method while placing them far away by another (Nei et al. 1993:249).

Recently, mitochondrial DNA (mtDNA) has become a useful tool for studying population relationships. A mtDNA marker called the nine base-pair deletion, found in East Asia, the Pacific, and North and South America, is of particular relevance here. So far, the findings on the deletion have been of greater interest for the Pacific than for Southeast Asia (Gibbons 1994; Harihara et al. 1992; Melton, personal communication). On the basis of preliminary sampling, the deletion is absent from New Guinea highlanders. It is relatively rare in Northeast Asians and aboriginal Australians. It is fairly common (frequencies between 20 percent and 50 percent) in aboriginal Taiwanese, Filipinos, Malays, Malayan aborigines (Orang Asli), Javanese, Lesser Sunda and Molucca groups, and coastal New Guineans. The Aeta of the Philippines and Polynesian groups have much higher frequencies (over 90 percent). Since a systematic survey of Mainland Southeast Asia is not yet available for this mtDNA deletion, these data are not informative about the genetic relationship of Mainland to Island Southeast Asia. They do, however, show a relationship between Island Southeast Asia and some Pacific groups, presumably reflecting diffusion events of recent millennia.

Given this general genetical background, I turn now to a consideration of the presence or absence of rare or geographically restricted alleles in defined Southeast Asian groups. Few such alleles are informative on the question of an ancient Southeast Asian biological unity. The best-studied eleven such alleles are discussed below.

Rare variants that can be informative about Southeast Asian prehistory include regionally restricted ones and a few that are more widespread. For example, a worldwide variant that "disappears" in Southeast Asia or the nearby Pacific may hint at an important corridor of expansion or migration, involving ancient groups. However, low-frequency variants found in other parts of the world that also occur patchily throughout Southeast Asia are not informative. They may have been brought to Southeast Asia by invasions or through trade in historical times.

Five regionally restricted genetic variants are informative for Southeast Asia and are discussed below: hemoglobin Constant Spring (Hb*CoSp), hemoglobin E (Hb*E), ovalocytosis (Ov*), allele 9 of phosphoglucosyltransferase 2 (PGM2*9), and allele 6 of peptidase B (PepB*6). One East Asian–Amerind variant that disappears in Southeast Asia is discussed: transferrin D Chinese (Tf*DCChi). One East Asian–Pacific variant is discussed: allele 6 of glutamic pyruvate transaminase (GPT*6). Five worldwide variants are discussed: alleles 6 and 7 of phosphoglucosyltransferase 1 (PGM1*6 and PGM1*7), allele 2 of adenylate kinase 1 (AK1*2), allele 2 of peptidase B (PepB*2), and Rhesus d (Rh*d); of these five, all but PepB*2 and Rh*d disappear in Southeast Asia. Rh*d is the only one of the 12 variants discussed that is not informative. Many other alleles are also not informative: some have not been well studied; others occur in robust frequencies in all populations studied;

TABLE 1. GENETIC VARIANTS DISCUSSED IN THE TEXT

A. *Non-enzyme Proteins*

1. *Hemoglobin*: a red-cell protein having two alpha and two beta chains. Hb*CoSp (Constant Spring) has the alpha chain elongated.
2. *Transferrin*: a serum protein. Tf*DChi is a structural variant in the protein.
3. *Ovalocytosis*: affects red-cell membrane shape. Ov* is a membrane protein variant.

B. *Enzyme Proteins*

1. *Adenylate kinase-1*: in muscle and red cells. AK1*2 is a structural variant.
2. *Glutamic pyruvate transaminase*: soluble protein, in liver. GPT*6 is a structural variant.
3. *Peptidase B*: in red cells. Both PepB*2 and PepB*6 are structural variants.
4. *Phosphoglucomutase-1*: enzyme important in sugar metabolism. Both PGM1*6 and PGM1*7 are structural variants.
5. *Phosphoglucomutase-2*: important in sugar metabolism. PGM2*9 is a structural variant.

C. *Other*

1. *Rhesus blood group complex*: antigen. Rh*d underlines the Rh-negative blood type.

Note: For further information, see McKusick 1990.

still others have been found in only one population or, like Rh*d, have a low-frequency, patchy distribution.

Table 1 provides some general information on the alleles under discussion. Population data on these alleles have been obtained from standard compilations and specialized studies, all of which report the size of the samples tested. Most sample sizes for the populations studied were in the usual range for such genetic surveys, that is, >100. For small ethnic groups, sampling usually included all people available.

For convenience, I discuss genetic relationships in Southeast Asia in terms of subregions, as illustrated in Figure 1. Moving from west to east, the first subregion, TK, corresponds to the Tai-Kadai language area; most of the data for this category comes from Thais in Thailand. The second subregion, AA, corresponds to the Mon-Khmer and Viet language areas of Austroasiatic, for which Cambodians and Vietnamese provide the bulk of the data. The third subregion, Asl, corresponds to the Asian language area of the Malay Peninsula, with data from the Semang, Temiar, and Semai peoples. The fourth subregion, WMP, corresponds to the Western Malayo-Polynesian language area. The populations surveyed in this largely insular subregion include the Temuan and Malays of West Malaysia, western Indonesians, North Borneans, and Filipinos. The next insular subregion, CMP, corresponds to the Central Malayo-Polynesian language area, covering various islands to the east of Bali and Lombok. Next comes the New Guinea subregion, restricted here to Papuan language speakers (Pap). The penultimate subregion is Australia (Aus), corresponding to the Australian aboriginal language area. Finally, because of the suggestion that Taiwan is the ancestral home of the whole Austronesian language group (Bellwood 1985), I also include a Taiwan (Twn) subregion, corresponding to the Taiwan aboriginal language area.

As shown in Table 2, 10 of the 12 genetic variants under consideration occur in the TK, AA, or Asl subregions of Mainland Southeast Asia. The other two, PGM2*9 and GPT*6, are known only from Island Southeast Asia to New Guinea. Among the 10 former alleles, 6 diminish in either the WMP or the CMP parts of Indonesia (and are not known from Taiwan), and 3 span the Malay Peninsula (Asl)

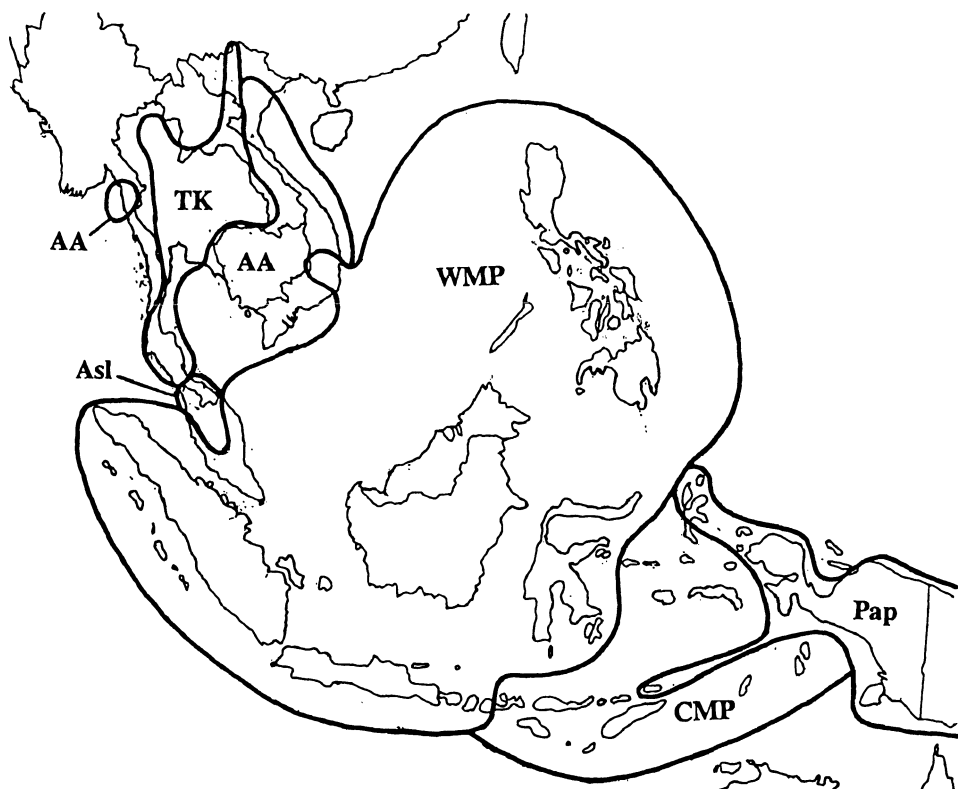


Fig. 1. Southeast Asian subregions and nearby areas. TK, Tai-Kadai language subregion; AA, Mon-Khmer and Viet language subregions of Austroasiatic; Asl, Aslian language subregion of Austroasiatic; WMP, Western Malayo-Polynesian subregion; CMP, Central Malayo-Polynesian subregion; Pap, Papuan subregion of New Guinea.

to New Guinea (Pap). Rh*d occurs sporadically throughout Southeast Asia and in Australia and is the only one of the 12 variants also to be found in Taiwan aborigines.

Overall, the data in Table 2 indicate a general easterly trend of these genetic variants, a lack of genetic relatedness between Taiwan aborigines and Southeast Asia, and more genetic relatedness between Southeast Asia and New Guinea than between Southeast Asia and Australia.

Because the WMP subregion contains 11 of the 12 variants under consideration and is the center of the west-to-east corridor of Southeast Asia, the question arises as to the source of the variant alleles in WMP. Table 2 suggests that alleles Hb*CoSp, PGM1*7, PGM1*6, AK1*2, Tf*DCh, and Hb*E originated in the Asian mainland. Little information is available on the mainland occurrence of the next five alleles in the table (Ov*, PepB*2, PGM2*9, GPT*6, and PepB*6), but they all occur in New Guinea. Ignoring PepB*2, which has not been reported from the WMP subregion, the other four may have arrived in WMP from New Guinea. The distribution of Rh*d, however, does not show a geographical trend.

Several methods exist to quantitate the similarity of the WMP subregion with others nearby, using presence/absence data (Cheetham and Hazel 1969). To illus-

TABLE 2. PRESENCE/ABSENCE OF VARIANT HUMAN ALLELES IN SOUTHEAST ASIAN SUBREGIONS, IN WEST-TO-EAST FORMAT, PLUS TAIWAN

	TK	AA	ASL	WMP	CMP	PAP	AUS	TWN
Hb*CoSp	+	—	+	+	—	—	—	—
PGM1*7	+	nd	+	+	—	—	—	—
PGM1*6	+	nd	+	+	—	—	—	—
AK1*2	+	+	+	+	+	—	—	—
Tf*DChi	+	+	+	+	+	—	—	—
Hb*E	+	+	+	+	+	—	—	—
Ov*	nd	nd	+	+	+	+	—	nd
PepB*2	nd	nd	+	—	+	+	—	nd
PGM2*9	nd	nd	—	+	+	+	—	nd
GPT*6	—	nd	nd	+	—	+	—	nd
PepB*6	nd	nd	+	+	—	+	+	nd
Rh*d	+	+	—	+	+	—	+	+

Key: nd, no data; TK, AA, and Asl are Mainland subregions; WMP and CMP are Island subregions; Pap, Papuan groups in New Guinea; Aus, Australian aborigines; Twn, Taiwan aborigines. Positive (+) and negative (—) refer to the reported presence or absence of an allele in a subregion.

Sources: Bowman et al. 1971; Lie-Injo et al. 1974; Lie-Injo 1976; Livingstone 1985; Mourant et al. 1976; Omoto et al. 1978; Omoto 1984; Roychoudhury and Nei 1988; Saha et al. in press; Sofro 1982; Tills et al. 1983.

trate one method, consider the fact that WMP and TK share eight allelic tests (Table 2), with seven tests being jointly positive. This produces a similarity estimate of 88 percent. Likewise, with five tests being common to WMP and AA, four of which are jointly positive, the similarity estimate is 80 percent. By the same reasoning, similarity estimates for WMP with Asl, CMP, Pap, Aus, and Twn are 73 percent, 50 percent, 33 percent, 17 percent, and 8 percent, respectively. According to these estimates, Mainland Southeast Asia (TK, AA, and Asl) is more similar to the WMP subregion than are areas to the east (CMP, Pap, or Aus). The findings suggest that Mainland Southeast Asian genetic variants spread into Island Southeast Asia quite successfully, even though some were lost by chance or other mechanisms on the eastward path.

These west-to-east genetic associations, while suggestive, are insufficient to establish a prehistoric movement of people. The west-east gene sharing might reflect, for example, similar latitudinal selection pressures. But this possibility seems to be remote inasmuch as the genes under discussion encompass a wide range of biochemical functions that are unlikely to be coordinately selected.

CULTURE

In parallel with genetic traits, a few cultural traits link Mainland and Island Southeast Asians. An early event in material culture is the spread of the blowpipe from some unknown locus throughout Mainland and Island Southeast Asia and into New Guinea, but not into Australia or Taiwan (Bellwood 1985). This distribution coincides with that of the genetic trait called ovalocytosis, discussed in the previous section.

The thunder god, whether named Karei or something else, is part of a complex

of beliefs about the natural and social world that also links Mainland and Island Southeast Asia. The complex has been recorded for Miao-Yao speakers in Laos and Vietnam (two groups), the Andamanese, Austroasiatic speakers in Vietnam (two groups), Aslian speakers (three groups), Western Malayo-Polynesian speakers on the mainland (two groups), in the Mergui Archipelago (one group), in Borneo (eight groups), and in the Philippines (five groups) (Blust 1981; Howell 1984; Lebar 1972; Lebar et al. 1964). One component of this belief system, that mockery of animals can cause harm to humans, is common among Western Malayo-Polynesian speakers (the WMP subregion) and also is recorded for Central Malayo-Polynesian speakers (CMP subregion) in northeast Lembata (Lomblen), an island near Timor (Barnes 1974).

A cultural trait that spans Mainland Southeast Asia but does not, as far as I know, reach the insular area is the notion of the soul as a butterfly. It is found in the Naga of Assam and in the Burmese, both Sino-Tibetan speakers, in the Mon, Mon-Khmer speakers, and in the Aslian-speaking Semang of Malaya (Lebar et al. 1964). A search for this trait in other groups might reveal a broader geographical range, but, for now, its distribution resembles those of the genetic traits Hb*CoSp, PGM1*7, and PGM1*6, as shown in Table 2.

A little-reported cultural trait that may have a fairly wide distribution is what I call the twin-belief complex, in which singleton human births are believed to be twins, with the placenta being the inviable co-twin. Aspects of this belief are found in Malaya, both among Aslian and among Western Malayo-Polynesian speakers, as well as among the Javanese, Balinese, and two groups in the Philippines (all Western Malayo-Polynesian speakers) (Baer unpubl.; Howell 1984; Laderman 1983, 1991). Also, Tambiah describes a Lao-speaking village in northeast Thailand in which spirit-possession curers may not eat a cow's placenta because it is considered "a kind of calf" (1970:319). However, Spencer (1949-1950:1172), writing about the world in general, states that "a mystical or magical notion often attaches itself to the afterbirth and the umbilical cord; many cultures regard this as a kind of double of the child." Unfortunately, he provides no examples.

Prehistorians have not so far identified any cultural traits that definitely link Mainland and Island Southeast Asia much before the last glacial maximum, with one exception. Earlier stone-age artifacts are evidently similar enough in design to indicate a recognizable cultural "tradition" of flake tools that goes back some 40,000 years in China, Thailand, and Sulawesi (Anderson 1987).

Overall, then, cultural traits offer some tantalizing glimpses of a common mainland-island world in Southeast Asia that may be quite ancient. By themselves, these commonalities may be considered as undated, and undatable, effects of the lateral diffusion of ideas. They can only be offered here as supporting evidence for human-genetic patterns in the region, which "diffuse" only by descent.

A similar caveat applies to the observation by Van Heekeren (1972) about hand stencils found on cave walls and other rock faces, typically made by splattering red ochre over a left hand held flat against the surface. Such stencils have been found in southwestern Sulawesi, the Moluccas, Timor, the north coast of New Guinea, and southeastern Australia. These stencils, then, show a distribution somewhat similar to those of the genetic variants PGM2*9 and PepB*6, discussed earlier,

as well as to the well-known ancient trickle of marsupials westward from the Australia–New Guinea area.

THE PREHISTORIC RECORD AND BIOGEOGRAPHY

In this section I attempt to relate the west–east distribution of genetic and cultural traits discussed earlier with fluctuating conditions on the continental (Sunda) shelf during the Late Pleistocene.

Thermoluminescence dating of sediments suggests human settlement of Australia by at least 50,000 B.P. (Roberts et al. 1990), presumably by way of Southeast Asia. Yet in Southeast Asia few remains of *Homo sapiens* have been firmly dated to 40,000 B.P. or earlier. Various rock shelters and caves in Southeast Asia that lack human remains do, however, contain flake tools, and in places also antler and bone tools, that date to 27,000, 37,000, and even 40,000 B.P. Such sites occur in southern Thailand, northern Borneo, and on Palawan Island (Jones 1989).

During the Pleistocene, an ice age occurred from about 80,000 to 12,000 B.P. Sea levels generally fluctuated between 40 and 70 m below those of today, according to Van Andel (1989), although at the last glacial maximum, around 17,000 B.P., the sea-level reduction was 120 m. In Southeast Asia, the low sea levels resulted in a large marine area, the Sunda Shelf, periodically becoming land (Roberts 1984). This Sundaland area—between Thailand, southern Viet Nam, Malaya–Sumatra–Java, and the northwest area of Borneo up to and including Palawan—may well have been a habitat rich in food resources, at least near its rivers, swamps, and coasts (Higham and Bannanurag 1992).

Sundaland probably reached its greatest extent—doubling in size—around 17,000 B.P. As the sea level fell on the shelf, vast new plains emerged. These plains sloped only 100 m or so from the vicinity of Bangkok to the distant coast, between Viet Nam and Borneo. They were transected by several rivers, draining—in most cases—into the South China Sea. Today's rivers—from the Mekong to the Chao Phraya, Pahang, Kapuas, and Lupar—would have been up to 1000 km longer during glacial maxima, carrying much larger water volumes and silt loads in their lower reaches.

I conjecture that with each expansion of Sundaland during the Late Pleistocene—roughly every 10,000 to 20,000 years—the new plains would at first have been swampy, with a mangrove fringe in many coastal and estuarine areas. The swamps very likely supported a variety of waterfowl, shellfish, palm groves, and plant foods such as taro. As the land area continued to enlarge, the ever-wet conditions (centered today on Malaya, Sumatra, and Borneo) would have become more continental, with seasonal rains. Whereas gallery forests would have colonized along the new river extensions, quite likely open parkland existed inland away from the rivers. The plains ecosystem would have provided an enormous habitat for birds and for grazing and browsing animals and their associated predators.

It seems reasonable to assume that land mammals such as pangolins, slow loris, monkeys, gibbons, sun bears, martens, otters, civet cats, mongooses, tigers, leop-

ards, elephants, tapirs, rhinoceroses, pigs, and deer may have lived on the Sunda plains (see Jones 1989; Medway 1969), as well as jungle fowl. In support of this view, most of these animals are found today in surrounding land areas—such as Thailand, Indochina, Malaya, Sumatra, Borneo, Palawan, and Java (Groves 1985; Heany 1985). In addition, extinct forms existing into the Late Pleistocene, such as stegodonts, may have thrived on Sundaland. Reptiles such as crocodiles, tortoises, and monitor lizards may also have been Sunda plain inhabitants.

The greater yam, native to Mainland Southeast Asia, is today a cultivated staple in parts of Taiwan, Mentawai, and Banggi. Native yams are also gathered by the Malayan Semang and other hunter-gatherers in Southeast Asia (Endicott and Bellwood 1991). Yams, bananas, tree fruits, palms, freshwater fish, and the swamp-adapted wild taro may have been predictable food sources on the expanded Sunda plain. Palms could have provided fruit, “heart,” and pith starch. Notably, taro was already part of the human diet by 28,000 B.P. in the Solomon Islands (Loy et al. 1992). And foraging is still widespread in Southeast Asia: Laderman (1983) reports 72 species of wild plants consumed by Malays on the east coast of Malaya in the 1970s.

These postulated Sundaland resources—both animal and plant—could have attracted early humans. While a sizeable human population may have lived on the expanded Sunda plains during glacial periods, the sea transgressions of interglacial periods would have forced Sunda-plains groups up to higher ground. The fact that most human deposits in caves in Malaya and nearby areas go back not much more than 10,000 years suggests to me that groups relocated to higher ground between 17,000 and 10,000 B.P., at which time the sea level stabilized. However, human occupation of higher-ground sites in the Sunda region is clearly documented for much earlier times, one site in southern Thailand being more than 37,000 years old (Anderson 1987). Indeed, this site was unoccupied after 27,000 B.P. and only reoccupied around 10,000 B.P. In contrast, a site on Sulawesi—an off-shelf island—*was* occupied between 31,000 and 10,000 B.P. (Jones 1989).

Before the advent of reliable water transport (at least 40,000 B.P.), Sunda-plains groups may have relocated in different directions when the sea level rose, because of the river-drainage pattern of the plains: those between the Red and Mekong drainages moving toward Indochina, those between the Chao Phraya and Pahang moving to the Malay Peninsula, and so on.

While any retreat to Indochina, Borneo, and Sumatra provided a large hinterland, a pullback to the Malay Peninsula or to Java did not. Nor did the Malay Peninsula, for example, contain large lowland areas such as the lower reaches of the Mekong and Chao Phraya rivers today (Hutchison 1989). Thus the human and other populations of this Malayan sector of a shrinking Sundaland must have (1) contracted, (2) adapted to a new ecosystem (inland uplands), (3) gone extinct, or (4) moved northwest into Burma–Thailand or southeast along the Sunda chain of Indonesian islands. Overall, the waxing and waning of Sunda shelfland may have had the effect of repeated easterly breakouts from Sundaland at weak (least populated and least competitive) points: via Java to eastern Indonesia and via Borneo to the Philippines. Both of these “exits” would have involved minor sea travel. As Australia was settled by a sea crossing, however, travel over the warm, shallow seas of Southeast Asia seems a reasonable assumption.

The abundant marine resources of Southeast Asia were possibly also important

to people during the Late Pleistocene, including as they did fish, shellfish, egg-laying beach turtles, and algae (rich in vitamins and minerals) (Abbott 1991). Indeed, the triangle formed by the Philippines, the Malay Peninsula, and New Guinea is said to contain the world's most diverse marine fauna (Briggs 1987).

Human access to marine resources and intertidal zones was highest during the Pleistocene when the Sunda plains were contracted; then the length of shoreline was greatly increased. At those times coastal groups could expand all the way back to the Chao Phraya outlet of today's Gulf of Siam. They could also follow the receding shoreline northeast toward the Philippines or southeast along the Sunda Island Arc. Indeed, coastal groups may well have led the way into the northeast and southeast from Sundaland, pioneering ahead of hinterland-based groups (see also Solheim 1984–1985). Bowdler (1990) has suggested a similar scenario for early Australian settlement.

Today's distribution of Mainland Southeast Asian human genes east into Island Southeast Asia may be related to the migratory pumping action I have hypothesized for the ice-age expansions and contractions of Sundaland. Likewise, today's mainland-to-islands faunal distributions are consistent with such a mechanism.

The land-locked vertebrates on the Sunda shelf and beyond it in the Philippines, Sulawesi, and the Lesser Sunda Islands have strong mainland Asian affinities (Cranbrook 1981). Fish intolerant of salt water, for instance, show evidence of a "Sundaic radiation" from the mainland. In general, fewer of these freshwater fish reached Java than reached Borneo, Sumatra, or Malaya. Beyond these Sundaland islands, land-locked Asian mammals that are not commensal or symbiotic with humans are rare. Large meat eaters such as tiger, panther, and bear never made it off the Sunda shelf.

The partial extinction of the Pleistocene megafauna of Southeast Asia, including stegodonts, may have been due to environmental changes rather than over-hunting (Cranbrook 1981; Jones 1989). Medway (1972) reported that of 200 extinctions globally in the late Pleistocene, only 11 occurred in Southeast Asia. Various explanations have been proffered for this Southeast Asian anomaly, but one possibility is that the majority of early humans in the region were coastal dwellers, rather than inland "big game" hunter-gatherers. Large numbers of shell middens in the region attest to the long-term exploitation of the land-sea interface by humans. Indeed, in other parts of the world human collecting of mollusks dates to well over 100,000 B.P. (Masters and Flemming 1983).

SUMMARY AND CONCLUSIONS

Although current information on the prehistory, human genetics, human ecology, and anthropology of Southeast Asia is far from comprehensive, enough is now available to begin to take a holistic approach to human biocultural diversity in the region. This approach can provide a baseline for future studies, especially those ongoing in the realm of molecular genetics, archaeology, and perhaps even ecology.

By discussing human genetic and cultural variation along with biogeography for Southeast Asia, I have attempted to show that a major west-east corridor of some antiquity exists in the region. Whereas language distributions do not

show a west-east trend, notable genetic variants, cultural traits, and faunal distributions do. This trend, in my opinion, is an important consideration for our future understanding of biocultural diversity in Southeast Asia and its ancient causes.

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ABSTRACT

Southeast Asians share some unifying traits within their biocultural diversity. In this report I discuss the hypothesis that temporal and spatial aspects of this unity reflect human settlement in Southeast Asia from the Thai–Indochina area out through Indonesia, and on to Australia–New Guinea, starting perhaps 40,000 or more years ago. Several rare or regional genetic variants are distributed from the mainland eastward to Indonesia, or on to New Guinea. Several cultural traits also show an eastward trend, suggesting that Island and Mainland Southeast Asia are culturally related in terms of a preagricultural past. Faunal distributions suggest that most of Indonesia's extant land vertebrates arrived prehistorically from continental Southeast Asia across a landmass now under water on the Sunda Shelf. This range expansion of animals, and also of humans, through Island Southeast Asia may have been the result of the periodic expansion and contraction of exposed land on the Sunda Shelf, caused by Pleistocene glaciations at higher latitudes. Together, these genetic traits, cultural motifs, and biogeographical considerations support the scenario of a pre-Holocene human expansion from the Thai–Indochina area through Indonesia. In contrast, today's language affiliations in Southeast Asia do not conform well to an eastward trend; they may be the products of recent, Holocene events. KEYWORDS: Sundaland, rare genetic traits, cultural traits, faunal distributions.